

FOOD CONSUMPTION RATES AND COMPETITION IN A COMMUNALLY FEEDING SOCIAL SPIDER, *STEGODYPHUS DUMICOLA* (ERESIDAE)

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ABSTRACT. A major factor which affects an animal's consumption rate is competition for food items. Competition usually results in a drop in consumption rate; however, this may be counteracted if the animals can exploit the foraging efforts of others, as could occur in social spiders when feeding on the same prey item. Spiders digest prey extra-orally and might utilize the enzymes or digesta produced by other individuals feeding from the same prey item. We investigated prey consumption in the social spider *Stegodyphus dumicola* to determine if the rate of consumption of individual spiders changed in the presence of competitors. We found that when one spider fed on small prey, food consumption rate decreased with feeding duration. When the prey was larger in relation to the spider there was an initial delay in consumption. There was no apparent advantage for a second spider to feed on a prey item already being consumed: the second spider fed for less time and gained less mass. These results indicate that social spiders compete during the process of food ingestion and the presence of another spider reduces the value of the prey item to a subsequent forager.

Keywords: Competition, sociality, foraging

Foraging theory indicates that the rate at which food is consumed at a patch strongly influences the residual value of that patch to an animal (Krebs et al. 1974; Charnov 1976; Iwasa et al. 1981). Competition among conspecifics can reduce consumption rate by reducing the residual amount of food in a patch available to the forager, or by reducing the amount of time available for foraging owing to time lost in direct physical confrontation (Sasvari 1992).

In group-feeding social species, competition during foraging and feeding is expected to be less extreme than in solitary species. Social spiders are those that live in communal webs in which there are no individually defended territories (D'Andrea 1987; Avilés 1997; Whitehouse & Jackson 1998). Social spiders cooperate in capturing prey which is then consumed by a group of individuals. By cooperating, they can handle larger prey than most similar-size solitary species (Nentwig 1985; Rypstra & Tiley 1991; Rypstra 1993; Pasquet & Krafft 1992).

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Spiders feed using extra-oral digestion in which they pump enzymes into the body of the prey and then ingest the emulsified contents (Collatz 1987; Cohen 1995). Extra-oral digestion affects the rate at which food can be consumed by such a predator during a feeding bout. As enzymes need time to digest prey, the predator may not ingest much food in the initial stages of feeding, but it can consume food at a fast rate later on, once the prey is digested. In social spiders many individuals can feed on the same prey, which may mean they have access to each other's enzymes. This could result in spiders exploiting enzymes and digesta of other individuals (Ward & Enders 1985; Whitehouse & Lubin 1999). In this situation, the presence of conspecifics feeding concurrently on a food item may actually increase the value of the food item and increase the rate of consumption for the "exploiting" spider.

The timing of feeding by an individual within a group foraging event could influence its rate of prey consumption. If the prey is initially digested slowly and then later digested quickly, it may be advantageous to feed from the prey later in the foraging event, after

other spiders have injected enzymes and digestion has begun. Alternatively, if the prey is digested quickly and consumption is initially fast but quickly drops off, then the first to feed will gain the most and it may be advantageous to lead the attack on the prey in order to secure the best feeding position. Attacking first, though, is potentially hazardous. The attacker must subdue the prey, possibly depleting its poison reserves and putting itself at risk. Thus, the rate of prey consumption can influence both the attack and the feeding strategies of group-feeding spiders. Factors which have been shown to affect consumption rate in extra-orally digesting predators include the size of the prey relative to the predator (Cohen & Tang 1997; Erickson & Morse 1997), the type of prey involved (Leborgne et al. 1991), and the size of the feeding group (Ward & Enders 1985).

We studied the feeding behavior of the social spider *Stegodyphus dumicola* (Eresidae) to determine the influence of the presence of a conspecific on the trajectory of prey consumption. *Stegodyphus dumicola* occurs in southern Africa in colonies of up to several hundred individuals. The spiders cooperate in nest construction, care of young and prey capture, and readily feed together in large groups (Seibt & Wickler 1988; Wickler & Seibt 1993). We examined the consumption rate of "groups" consisting of only two animals feeding on small grasshoppers of half to two-thirds their body size and compared consumption rates of members of a pair and of solitary individuals. While a group size of two individuals is unusual, such groups do occur in nature (Henschel 1991/1992); and even in larger nests, small prey items are often attacked by only a few individuals (Lubin pers. obs.).

METHODS

Colonies of *S. dumicola* containing juveniles were collected in Namibia in January 1996 and housed in Sede Boker, Israel, in a climate-controlled room at 27 °C. and a photoperiod similar to outside conditions. Experiments were conducted from July 1996 to March 1997, and all spiders used in the experiments were derived from the same colony. The spiders were all juvenile females weighing about 40 mg, or about two-thirds adult

size. Voucher specimens are deposited at the Mitrani Department for Desert Ecology.

Food consumption pattern of single spiders.—Consumption rates were determined for spiders feeding alone in two tests. Because the tests were separated by a few weeks, spiders in the second test were larger than those in the first. In the first test, 51 individuals of similar body size were drawn from the colony and put in individual plastic containers (a cylinder 30 cm long, diameter 12 cm) with supports for web building, where they were given seven days to acclimate. After a week, each spider was weighed on an analytical balance to the nearest 0.1 mg, and then fed one grasshopper nymph. We recorded the time until the spider attacked the prey, and the length of time the spider fed (excluding pauses in feeding). Different individuals were allowed to feed for predetermined durations (15, 30, 60, 90, 120, 180, and 240 min) after which feeding was stopped and each spider was reweighed.

In the second test, conducted concurrently with the test of pairs of spiders (see below), 23 individuals were allowed to feed for different durations, as in the first test. There was a small, but significant difference in body sizes of spiders between the two tests ($t = -4.6$, $df = 72$, $P < 0.001$; average body mass in the first test: 42.15 ± 5.7 mg, second test: 48.6 ± 5.3 mg). The prey mass was increased in the second test ($t = -11.6$, $df = 72$, $P < 0.001$; average prey mass in the first test: 19.3 ± 3.6 mg, second test: 29.5 ± 3.2 mg). The ratio of prey mass to spider mass was higher in the second test (0.61 ± 0.05) than in the first (0.465 ± 0.1 ; arcsin transformed ratios, $t = -6.85$, $df = 72$, $P < 0.001$).

Food consumption of pairs.—Twenty-one pairs of spiders were matched for size (body mass: 46.7 ± 6.3 mg; average mass difference between pairs = 3.5 mg, range 0–14.6 mg). To distinguish between pair members, bee numbers (numbers designed for use in apiaries) were glued to the abdomen with transparent nail polish. The pairs were placed in plastic containers and left for seven days to acclimate. Before the experiment each spider was weighed, and each pair was given one grasshopper nymph. We recorded the time until the first spider attacked the prey, and the duration of feeding (excluding pauses in feeding). Once the first spider had fed for a pre-

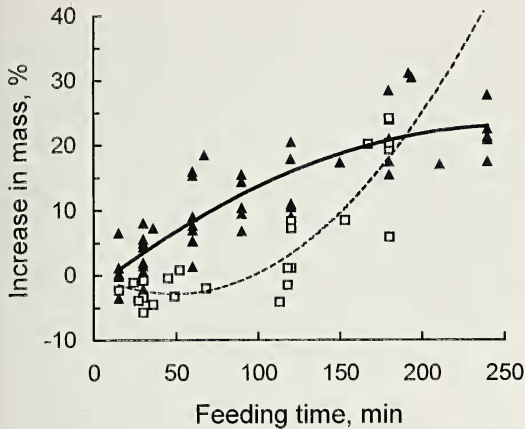


Figure 1.—Relative consumption rates (% increase in body mass) of spiders feeding alone: a comparison of two ratios of prey/spider mass. Filled triangles (▲), heavy line: low ratio = 0.465 ± 0.1 ; open squares (□), thin line: high ratio = 0.62 ± 0.07 . The polynomial regression of the low-ratio curve is: $y = -x^2 + 0.19x - 2.03$, $R^2 = 0.74$; the regression of the high-ratio curve is: $y = x^2 - 12x + 0.09$, $R^2 = 0.78$ (percentages were arcsine transformed for the regressions).

determined length of time (either 15, 30, 60, 90, 180, or 240 min) the experiment was stopped. If the second individual had begun to feed, we recorded the time it began to feed and the duration of feeding.

RESULTS

Food consumption pattern of spiders feeding alone.—The rate of food consumption by spiders feeding alone was examined in the two different tests. When spiders fed in the absence of conspecifics (first test), their body mass increased with the time spent feeding ($F_{1,23} = 39.8$; $P < 0.001$). However, there was a significant difference in mass gain between the first and second tests (ANCOVA: final body mass with initial mass as covariate, $F_{1,71} = 7.94$, $P = 0.006$; Fig. 1) which was caused by differences in the trajectories of mass increase experienced by the two groups. In the first test, the relative change in body mass was initially linear and began to asymptote after two hours. In the second test, the coefficient changed sign, and the spiders began to show an increase in body mass only after an hour of feeding. The difference between the two tests is explained in part by the different prey mass/spider mass ratios. In a general linear model, both prey mass and

feeding time were significant ($P < 0.001$, $n = 74$, with initial spider mass as covariate), together explaining 87.4% of the variance in final spider body mass for both tests.

Food consumption of spiders in pairs.—When all 21 pairs of spiders were considered, the trajectories of prey consumption of first and second spiders did not differ (ANCOVA, $P > 0.1$; combined regression, $y = 0.002x + 0.055$, Fig. 2). However, in 12 instances (57.1%), only a single spider of the pair fed. To establish whether one spider in a pair fed alone significantly more often than both spiders together, we needed to take into account the fact that we stopped spiders at different times after they started to feed. In the above 21 pairs, the maximum time taken for the first spider to attack the prey was 170 minutes. If we assume that the second spider responded to the prey in the same manner as the first spider, it should also have a maximum delay of 170 minutes before beginning to feed. Consequently, we removed the eight tests in which the experiment was stopped before it had run for 170 minutes. Of the remaining 13 tests, although the first spider fed in all of them, the second spider fed in only six instances (comparison of first and second spiders, Fisher's exact test, $P = 0.005$).

There was a short but variable delay between the attack of the first and second spider (median = 16 min, range = 8–164 min, $n = 9$). The first spider always fed longer than the second spider (Wilcoxon signed ranks test, $z = -2.67$, $P = 0.008$, $n = 9$), and there was a trend for the first spider to gain more mass than the second (Wilcoxon signed ranks test, $z = -1.7$, $P = 0.086$, $n = 9$). We tested for differences in the consumption rates of the first and second spiders that fed together by comparing the regressions of final body mass on net feeding time, with initial body mass as covariate. The consumption rate of the first spider was greater than that of the second spider to feed (ANCOVA, $F_{1,15} = 4.244$, $P = 0.057$).

Mass loss.—Some spiders lost mass during the feeding trials. The mass lost by the spiders was always larger than the measurement error due to weighing inaccuracy, which was calculated at 0.08 mg. In the first test with single spiders, four spiders (7.8%, $n = 51$) lost mass (median = -0.6 mg, range = -0.1 to -1.3 mg); all had fed for 15–30 min. Twelve spi-

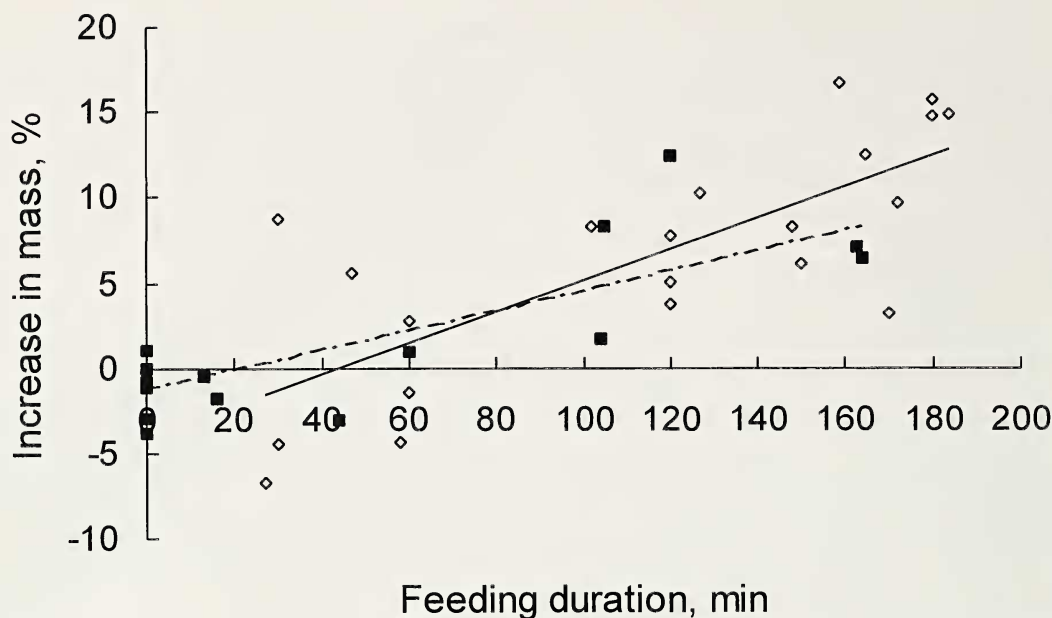


Figure 2.—Relative consumption rates of spiders feeding in pairs: percent increase in body mass against net feeding time of each spider. First spider to begin feeding: open diamonds (\diamond), solid line; second spider: closed squares (\blacksquare), dashed line. The regression equations are: first spider, $y = 0.092x - 3.98$, $R^2 = 0.58$; second spider, $y = x^2 + 0.06x - 1.13$, $R^2 = 0.655$ (arcsin transformed percentages).

ders lost mass in the second test (median = -1.25 mg, range = -0.2 to -3.0 mg), with feeding durations ranging from 15–118 min (median = 33 min). The feeding duration of spiders that lost mass was significantly shorter than of those that gained mass (median = 120 min, range 52–180 min; Mann-Whitney $U = 6.5$, $P < 0.001$, $n = 23$).

In spiders that fed in pairs, a decrease in body mass occurred in three first and nine second spiders. As the sample sizes were small, we used bootstrapping (Simon 1995) to determine the probability that the observed difference between the median mass loss in the two groups occurred by chance alone. There was no difference in mass loss between second spiders that fed ($n = 3$) and second spiders that did not feed ($n = 6$, $P = 0.21$). However, first spiders that fed and lost mass ($n = 4$) tended to lose more than second spiders that fed and lost mass ($n = 3$, $P = 0.087$) and more than the single spiders of the concurrent second test ($n = 12$, $P = 0.078$).

DISCUSSION

When solitary spiders fed on small prey items, their body mass increased with feeding time. In the first test with single spiders, using

relatively small prey (prey/spider mass = 0.465), the gain followed a typical curve of diminishing returns, similar to that shown by the spider *Zygiella x-notata* (Araneidae) feeding on cricket nymphs (prey/spider mass = 0.1–0.3; Leborgne et al. 1991). Thus, small prey items, less than half the mass of the spider, are rapidly depleted. Another spider attempting to feed on the same prey item would gain no advantage by waiting, and would obtain more food by joining early in the feeding bout.

With larger prey (prey/spider mass = 0.6), there was a delay in the spider's consumption, resulting in a feeding trajectory with the opposite sign to that above (Fig. 1). The lag before the initial increase in food intake might be due to the time necessary for enzymes to take effect in digesting the larger meal. The delay was more pronounced when spiders fed alone than when they fed in pairs. This suggests that the presence of conspecifics caused spiders to increase their consumption rate.

During the initial period on the prey, when venom and enzymes are presumably being pumped into the prey, spiders may even lose mass. Although sample sizes were small, mass

loss was greater in first spiders than in second spiders or spiders feeding alone (comparing only those individuals that lost mass). Thus, with large prey it may be advantageous for a second spider to join later and capitalize on enzymes injected by the first spider (Ward & Enders 1985). In tests with pairs of spiders, however, we found that the second spider tended to join early in the feeding bout. In spite of possible advantages of such "enzyme piracy" (Whitehouse & Lubin 1999), second spiders fed for less time than the first spiders and had lower consumption rates.

The advantage shown for the first spider to feed agrees with other studies of group feeding in social spiders. Willey & Jackson (1993) found that in *Stegodyphus sarasinorum*, when tested in groups of 10 individuals, spiders that attacked first fed for longer duration than those that arrived later. In *Stegodyphus mimosarum* (Ward & Enders 1985), the first spider of a pair to attack did not feed longer than its partner, but fed more frequently from the thorax and head of the prey, body parts which yield the highest reward (Robinson 1969), while its partner showed no feeding site preference. Likewise, in a group of five individuals of *S. dumicola* matched for size, the first spider that attacked the prey tended to obtain more food, but did not feed for longer (Whitehouse & Lubin 1999). In the latter study the individuals that gained the most mass were those that fed longest during the middle part of a foraging bout, although they also tended to initiate the attack (Whitehouse & Lubin 1999).

Competition over prey occurs in cooperative group-living spiders (Ward & Enders 1985, Whitehouse & Lubin 1999), but it is apparent mainly in differences in rates of food consumption. In the social *Stegodyphus*, there is little evidence of active competition in the form of aggressive interactions over prey. In this study, we found that when the prey item is smaller than the spider, often only a single spider will attack and feed, and when two individuals do feed together, the second obtains less food from the prey. The results of this study suggest that "piracy" of enzymes or digesta may occur, and that spiders may adjust the timing of feeding and their consumption rate to compensate for losses due to other individuals. These considerations as well as differences in possible trajectories of food con-

sumption, e.g., in relation to the relative size of prey and spider, may influence the decisions to join an individual feeding on a prey item. Further studies of the dynamics of group feeding and the physiology of food ingestion are needed to understand the costs and benefits of group feeding in social spiders.

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